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Aspects of the Life History of the Pacific Electric Ray, *Torpedo californica* (Ayres)

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Pacific electric rays (n = 198) were collected from central and southern California from July 1994 through January 1996 for studies on their age and growth, reproduction, and demography. Whole vertebral centra with graphite microtopography band enhancement were used for ageing. Average percent error and percent error were 6.5% and 4.9% among readings. Maximum age was an estimated 16 yr. The von Bertalanffy growth model provided the best fit and predicted an asymptotic total length of 1372 mm for females and 921 mm for males, and K was estimated to be 0.073 for females and 0.137 for males. Female and male reproductive status was determined using two and three criteria, respectively. Median total length-at-maturity, determined using a logistic response function, was 645 mm (age estimate, 6 yr) for males and 731 mm TL (age estimate, 9 yr) for females. Fecundity of one female was estimated at approximately 17 young per litter. Time of parturition could not to be determined. Instantaneous mortality estimates ranged from 0.096–0.277, depending on longevity estimates. Best age-based demographic analyses indicate that the Pacific electric ray population has a net reproductive rate per generation of 2.6–8.9, a generation time of 11.2–13.0 yr, instantaneous rates of change of 0.09–0.18, and finite rates of change of 1.09–1.20.

ELECTRIC rays (Torpedinidae) are aplacental viviparous elasmobranchs occurring in all major oceans. The Pacific electric ray, *Torpedo californica,* ranges from Sebastian Viscaino Bay, Baja California, to Queen Charlotte Islands, British Columbia, between 3 and 274 m (Miller and Lea, 1972), and a small fishery exists for biological and biomedical research specimens (Love, 1996).

Although information exists regarding the movement patterns and diet of the Pacific electric ray (Bray and Hixon, 1978; Lowe et al., 1994), little is known about its life span, age structure, growth rate, reproductive parameters, or demographic characteristics. The lack of information about the basic biology of the Pacific electric ray generated the following questions: (1) Are vertebrae useful as ageing structures for the Pacific electric ray? (2) Do Pacific electric rays grow slowly and live a relatively long time? (3) Do males and females differ in growth characteristics and size and age at maturity? (4) Do females have a relatively low fecundity? and (5) What are the possible demographic consequences of these age, growth, and reproductive estimates?

MATERIALS AND METHODS

Specimen collection.—Pacific electric ray specimens (n = 116 males, 186–842 mm TL; n = 81 females, 199–1020 mm TL) were obtained between August 1994 and January 1996 off central (Monterey Bay) and southern (Los Angeles Basin) California. Monterey Bay specimens were collected from otter trawl and fishery bycatch samples. Southern California specimens were hand or net collected by two commercial collectors.

Age and growth.—External examinations were conducted for all specimens. When possible, rays were sexed, weighed to the nearest 0.1 kg, and measured: disk width (DW, mm) and total length (TL, mm). Outer clasper length (from free tip of clasper to clasper origin) was recorded for males.

Five to seven vertebral centra were removed from the first through 25th vertebrae and prepared for age determination following techniques outlined in Martin and Cailliet (1988a). Centrum diameter (mm) was strongly and significantly (r^2 = 0.98, P < 0.001) correlated with total length, and the position of the centrum along the vertebral column did not affect the age estimate.

Several techniques for enhancing the banding pattern on the centra were assessed. Techniques that have proven useful for other species, alizarin red staining, silver nitrate impregnation, cedarwood oil staining, water immersion, (Cailliet et al., 1983), x-radiography (Martin and Cailliet, 1988a), and electron microprobe analysis (Cailliet and Radtke, 1987) did not significantly increase the readability of the banding pattern for Pacific electric rays on either whole or thin-sectioned vertebrae (Neer, 1998).

The graphite microtopography enhancement technique was used for all specimens following Parsons (1983). One whole centrum from each specimen was selected, and its face was lightly scraped with a no. 2 pencil, moving from the center toward the edge, to create a cone-shaped shaded area. The senior author read the number of observed bands three times using fiberoptic reflected light. All centra were aged three times, and an age consensus was achieved when at least two of the three age estimates agreed or with an additional readings. An index of precision (average percent error, APE) and percent error (D) were calculated to assess intrareader variability (Beamish and Fournier, 1981; Chang, 1982).

Following Cailliet et al. (1983) and Martin and Cailliet (1988a), we used ''bands'' (larger concentric marks, composed of groups of smaller ''rings'' observed on the vertebral face) to estimate age. Alternating bands would appear dark because of the graphite enhancement. One pair of light and dark bands was assumed to represent one year. Attempts to validate the temporal deposition of the banding pattern, including monthly centrum edge analysis and laboratory growth and oxytetracycline (OTC) and calcein internal marking studies, were unsuccessful.

One linear and three curvilinear (Gompertz, logistic, and von Bertalanffy) growth models were fitted to the age and length data using Microsoft Excel and Fishparm, a nonlinear curve-fitting software package using Marquardt's algorithm (Saila et al., 1988). Lowest mean square error (MSE) and r^2-values were used to determine which model had the best predictive value.

Differences in growth rates between males and females were assessed. Following Kappenman (1981), growth models were developed for the sexes separately and combined to determine which model best described the data. Differences between the sexes were also evaluated by testing parameters derived for the von Bertalanffy growth function (L_∞, K, and t_o) using a *t*-test with the confidence intervals provided by Fishparm (Cailliet et al., 1990).

Three methods were used to provide estimates of possible longevities: (1) the oldest fish aged in this study; (2) the formula 5 ln2/K, the time necessary to reach 95% of its asymptotic length (Cailliet et al., 1992); and (3) calculation of the age predicted by extending the mean growth rate to the L_∞ predicted by the von Bertalanffy model.

Reproduction and demography.—Male reproductive status was based on three criteria: (1) the relationship of clasper length to total length (Snelson et al., 1989); (2) clasper calcification (Yano, 1993); and (3) vas deferens coiling (straight, wavy, coiled, or a combination of two consecutive stages; Martin and Cailliet, 1988b). Outer clasper length was measured for all males. Clasper calcification was subjectively assigned to one of three categories based on ease of clasper bending: not calcified, partially calcified, and calcified. A specimen was considered mature if it met all of the following criteria: calcified claspers, coiled vas deferens, and a position above the upper inflection point on the clasper length—total length plot (~ 600 mm in this study).

The reproductive status of female specimens was based on two criteria: (1) diameter of ova (Abdel-Aziz, 1994); and (2) uterine width (Martin and Cailliet, 1988b). Females were considered mature if they contained ovarian ova > 10 mm in diameter or the uteri were differentiated from the oviducts (Abdel-Aziz, 1994). Fecundity was estimated using ovum counts and the examination of a single pregnant female. Time of parturition in Monterey Bay was examined by plotting the size of YOY rays relative to their month of capture. All ova present were measured along their longest axis to the nearest 0.1 mm.

Median total length-at-maturity (MTL) was determined following Mollet et al. (2000). A logistical model $Y = [1 + e^{(a + bX)}]^{-1}$ was fitted to our binomial maturity data (immature = 0, mature = 1) for males and females separately. MTL was calculated using the equation MTL = $-a/b$.

Estimates of total instantaneous mortality (Z) were obtained following Hoenig (1983), which predicts total mortality from maximum age of a species. This equation is designed to be used with mostly unexploited or lightly exploited fish stocks. Because there is only a minimal directed fishery for the Pacific electric ray, Z can be approximated to M (natural instantaneous mortality rate). Mortality estimates were calculated for the longevity estimates derived above.

An age-based life table was constructed to estimate the demographic parameters of generation time (G), net reproductive rate (R_o), and intrinsic rate of population change (r, refined using the Euler equation) following Cortés (1995) and Krebs (1985). The finite rate of change (e^r) was calculated using the refined *r*-values. Several combinations of longevity and mortality estimates were examined, providing a range of reliable estimates for each parameter.

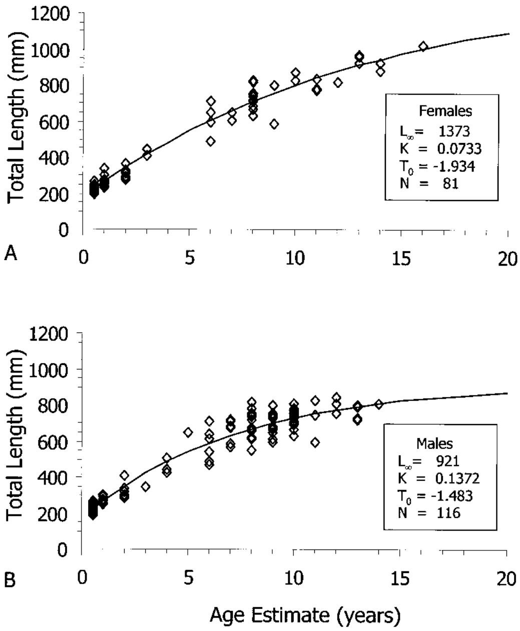

Fig. 1. Von Bertalanffy growth curves for female and male Pacific electric rays. Parameters are listed in the insert. (A) females; (B) males.

It was assumed that, once a female reached sexual maturity, the potential number of female offspring (m_x) remained constant, that she reproduced annually throughout her lifetime, and that the sex ratio at birth was 1:1 (based on data from one pregnant female).

RESULTS

Age and growth.—The total length-weight relationship was best described by a power curve of the form: $y = 0.00002x^{3.0213}$ ($r^2 = 0.99$) for females and $y = 0.00004x^{2.8753}$ ($r^2 = 0.98$) for males. A very strong ($r^2 = 0.96$–0.99) and significant ($P < 0.001$) linear relationship existed between total length and disc width.

The graphite microtopography technique was used for all 198 specimens. Average percent error (APE) and percent error (D) among the first three readings were 6.5% and 4.9%, respectively.

Size-at-age estimate plots indicated a nearly linear relationship between age and total length in both males and females (Fig. 1). Gompertz, logistic, and von Bertalanffy growth models also fit the data well. Although the Gompertz model had a slightly better fit (with the greatest r^2 and lowest MSE), the difference between it and the von Bertalanffy growth function (VBGF) was negligible. We used the VBGF to allow for comparisons with other elasmobranch species.

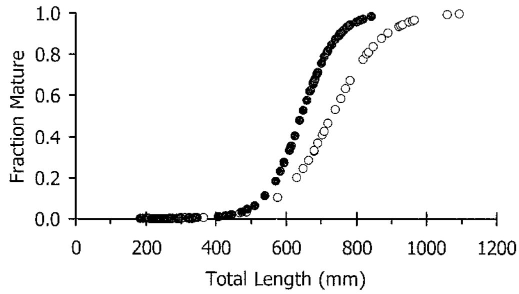

Fig. 2. Relationship between maturity and total length for the Pacific electric ray. A logistical model was fitted to the binomial maturity data (0 = immature, 1 = mature). o = females (n = 79); ● = males (n = 102).

Following Kappenman (1981), it was determined that von Bertalanffy models constructed for males and females separately described the data better than one model with both sexes combined (Fig. 1). Females reach their asymptotic length at a slightly slower rate (K = 0.07) than males (K = 0.13). The 95% confidence intervals around the predicted L_{oo} values for males (921 ± 107.4 mm) and females (1373 ± 288.2 mm) did not overlap, another indication that growth in this species was best described separately for males and females and that they exhibit sexual dimorphism.

Estimates of longevity varied widely with the method used (Table 1). An estimate of 47 yr was obtained using the 95% asymptotic length method, and an estimate of 24 yr was obtained by extending a mean growth rate to the L_{oo} predicted by the von Bertalanffy model and converting to age. The extreme longevity estimate of 47 yr is biologically unrealistic, and both calculated estimates exceed the maximum age of 16 determined for rays aged in the study.

Reproduction and demography.—MTL for male Pacific electric rays was 645 mm (Fig. 2). An

TABLE 1. SUMMARY OF DEMOGRAPHIC PARAMETERS [NET REPRODUCTIVE RATE (R_o), GENERATION TIME (G), INTRINSIC RATE OF INCREASE (r), AND FINITE RATE OF INCREASE (e^r)], CALCULATED FOR THE PACIFIC ELECTRIC RAY FOR THE THREE LONGEVITY AND RESULTING MORTALITY ESTIMATES OBTAINED IN THIS STUDY.

Longevity estimate	Mortality estimate	Demographic parameters			
		R_o	G	r	e^r
16	0.277	2.59	11.15	0.09	1.09
24	0.186	8.89	13.03	0.18	1.20
47	0.096	38.07	17.97	0.27	1.31

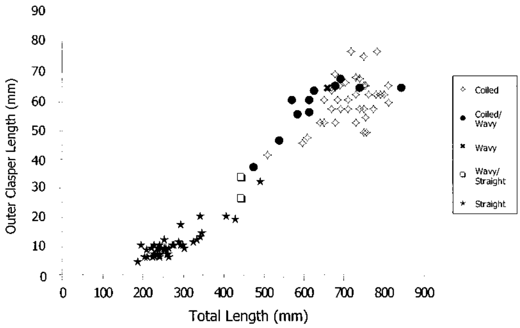

Fig. 3. Relationship of total length to outer clasper length for the Pacific electric ray, with categories of vas deferens coiling (n = 99).

abrupt change in the clasper length–total length relationship begins at ~ 450 mm TL (Fig. 3). Eighty-five percent of males > 645 mm TL displayed complete coiling of the vas deferens (n = 41), and 94% had calcified claspers (n = 34). The smallest mature male observed was 610 mm TL, and the largest immature male was 842 mm TL (~ 7 yr).

Female Pacific electric rays had a MTL of 731 mm (Fig. 2). Uterine width increased rapidly at 750 mm TL, with a maximum observed width of 50 mm in a 925-mm TL specimen. The smallest reproductive female was 721 mm TL, and the largest immature female was 756 mm TL. Eighty-four percent of females larger than 731 mm TL (n = 19) possessed ovarian ova greater than 10 mm diameter. A 1092-mm TL female with 8 mm eggs was most likely mature but obtained shortly after giving birth. Age at female MTL was estimated to be approximately 9 yr.

Estimates of fecundity varied with stage of female development. Both ovaries were functional, having approximately the same number of ova in each. Number of ova ranged from 0–55 per ovary, with the number increasing with increasing size of female rays. Two distinct ovum size classes often were present in each ovary. A single pregnant female (1000 mm TL) was taken in February and contained 17 near-term embryos (7 females, 10 males), ranging from 214–231 mm total length. Because young-of-the-year specimens (< 250 mm total length) were obtained year-round from Monterey Bay during monthly sampling, parturition may occur in all months.

Using the three longevity and mortality estimates, and the assumption of annual reproduction, demographic parameters varied widely (Table 1). Estimates of G ranged from 11.2–18.0 years. R_o-values ranged from 2.6–38.1 for this species. Intrinsic rate of increase (r) estimates ranged from 0.09–0.27, and e^r-values ranged from 1.09–1.31.

Discussion

Age and growth.—We feel confident in our age estimates even though Pacific electric ray vertebrae are very thin, fragile, deeply coned, and poorly calcified structures and despite the lack of validation of our age estimates. The graphite microtopography technique produced low APE, and D-values, providing some verification of the age estimates and the von Bertalanffy growth model parameter estimates seem sensible when compared to other elasmobranch species (Cortés and Parsons, 1996). In addition, our sample size was relatively large (n = 198), covered the known size range of this species, and both sexes were well represented.

Pacific electric rays could exceed our oldest age estimate of 16 yr of age. The largest individual examined was 1020 mm in total length, smaller than the maximum reported length of 1372 mm for females of the species (Eschmeyer et al., 1983) but very close to the asymptotic length (1373 mm, ~ 24 yr) predicted for females by the von Bertalanffy growth model. This estimated longevity of 24 yr is comparable to that of other species in this family. Female *Torpedo marmorata* may have a life span of approximately 20 yr, and males may live to approximately 13 (Mellinger, 1971). The lesser electric ray, *Narcine entemedor,* may exceed 11 yr for males and 15 yr for females (C. J. Villavicencio-Garayzar and G. M. Cailliet, unpubl.). These age estimates have not been validated, although C. J. Villavicencio-Garayzar and G. M. Cailliet (unpubl.) successfully used marginal increment analysis to document periodicity in the lesser electric ray. Attempts to validate the annual deposition of the banding pattern in the Pacific electric ray were unsuccessful.

The Pacific electric ray is sexually dimorphic, with females reaching a larger size than males (1373 mm TL vs 921 mm TL) and doing this at a slower rate (K = 0.07) than males (K = 0.13). These trends have been observed in other elasmobranch species (Martin and Cailliet, 1988b; Cailliet et al., 1992; Abdel-Aziz, 1994).

Reproduction and demography.—The onset of male sexual maturity occurs at approximately 7 yr of age, or 70% of the predicted total length obtained by males. Male Pacific electric rays have a MTL of 645 mm. Marbled electric ray, *T. marmorata,* males reach sexual maturity at 5 yr (Mellinger, 1971).

Female Pacific electric rays reach sexual maturity at 9 yr of age (MTL of 731 mm), or approximately 53% of their reported maximum size. This is similar to the marbled electric ray, *T. marmorata,* which reaches maturity at 10–15 yr at 55–68% of its maximum size (Mellinger, 1971; Capapé, 1979; Abdel-Aziz, 1994). The estimate for the spotted electric ray, *T. ocellata,* is slightly lower at 41–53% of maximum total length (Quignard and Capapé, 1974).

Fecundity of the Pacific electric ray (17) is similar to that of other electric ray genera and species. Studies indicate fecundities between 4 and 18 young per female (Michaelson et al., 1979; Villavicencio-Garayzar, 1993, Abdel-Aziz 1994). The fecundity estimate reported here, 17 young per female, is one of the highest reported for batoids (Martin and Cailliet, 1988b; Timmons and Bray, 1997); however, additional fecundity information (both ovarian and uterine) is necessary to further examine the apparent trend of ovarian ova number increasing as total length increases. An increase in fecundity with body size has been observed for *T. torpedo* and *T. marmorata,* as well as for several species of sharks (Mellinger, 1981; Smith and Abramson, 1990). Unfortunately, no reproductive cycling or gestation information was collected during this study. Mellinger (1971) and Capapé (1979) reported a 2–3 yr reproductive cycle for female *T. marmorata*; with males having an annual cycle. Gestation estimates for the genus *Torpedo* range from 4–12 months (Quignard and Capapé 1974; Capapé, 1979; Abdel-Aziz, 1994).

Mortality estimates (z) ranged from approximately 0.096–0.277, depending on the longevity estimates used and all fit within the range published by Hoenig (1983). The mortality estimates of 0.277 and 0.186 seem most biologically realistic for the Pacific electric ray. From the demographic parameters calculated using the two most biologically realistic estimates of longevity (16 and 24) and mortality (0.277 and 0.186), population growth of the Pacific electric ray appears to be considerably higher than values reported for most other elasmobranch species (Table 1; Cortés and Parsons, 1996). Our most realistic estimates indicate that this population may be capable of increasing between 9% and 20% per year, however potential density-dependent effects on population growth were not included in our analyses. Our estimates are most comparable to those of the bonnethead (r = 0.283) and Atlantic sharpnose (r = 0.044) sharks, two relatively short-lived species (Cortés, 1995; Cortés and Parsons, 1996); however, other demographic analyses of batoids have not been published

Results of this study indicate that Pacific electric rays appear to be similar to other elasmobranchs in being relatively long-lived, having low fecundity, and a late age at sexual maturity. However, more detailed information regarding age validation, parturition season, reproductive cycles, and natural mortality is needed to refine the estimates presented here.

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